STUDIES ON DIFFERENT JHUM (SLASH AND BURN AGRICULTURE) PATTERNS AND POPULATION DYNAMICS OF A FEW WEEDY SPECIES

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We certify that the thesis entitled "STUDIES ON DIFFERENT JHUM (SLASH AND BURN AGRICULTURE) PATTERNS AND POPULATION DYNAMICS OF A FEW WEEDY SPECIES" submitted by Shri Satya Prakash Singh Kushwaha, M.Sc., for the degree of Doctor of Philosophy of the North-Eastern Hill University, Shillong, embodies the record of original investigation carried out by him under our supervision. He has been duly registered and the thesis presented is worthy of being considered for the award of the Ph.D. degree. This work has not been submitted for any degree of any other university.

27/6/81

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DEDICATED

TO

MY PARENTS

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(S.P.S. KUSHWAHA)

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PREFACE

The results presented in the present thesis start with a consideration of three types of land use practices in the north-eastern hill region, namely, (i) slash and burn agriculture with jhum cycles of 5 and 10 years, (ii) valley cultivation of rice and (iii) terrace cultivation of rice which has recently been suggested as an alternative to jhum by the local governmental agencies. The various weeds coming up during cropping have been considered along with a study of the economic yield patterns.

The subsequent three chapters deal with the biology and population dynamics of two important early successional weeds namely _Eupatorium odoratum_ L. and _Imperata cylindrica_ (L.) Beauv. coming during and after jhum. These studies pertain to population dynamics during secondary succession after slash and burn agriculture which has been contrasted with a late successional weed, _Scleria tessellata_ Willd. The next two chapters deal with competition between the plants of rhizome versus seed origin in _I. cylindrica_, followed by a study on competition between _I. cylindrica_ and _E. odoratum_, the former of rhizome origin and the latter of seed origin as they come up in nature after jhum. This study considers the two nutrient levels as soil nutritional changes are significant after slash and burn. This is followed by studies on the behaviour of _I. cylindrica_ and _E. odoratum_ in response to different light and water regimes.

The thesis starts with a general introduction which includes an extensive study of literature and ends with bibliography. Some repetition in writing up of the chapters could not be avoided as they are written as independent papers for publication. Through these studies it is hoped to get an understanding of the biological equipments of the weedy species.

GENERAL INTRODUCTION

Population ecology:

The history of population research dates back to the time of Malthus (1798) who observed that a population exhibits a tendency to multiply geometrically as a result of the "passion between the sexes". The publication of a book "An Assay on the Principles of Population as it Affects the Future Improvement of Society" marked the beginning of the modern studies on populations. Acknowledging the ideas gained from Malthusian postulates, Darwin (1859) in his book "Origin of Species", emphasized the importance of the individuals in a population making frequent references to their numerical strength.

Verhulst (1838) proposed the first logistic mathematical expression of population growth under limiting means of subsistence which was later presented by Pearl and Reed (1920) in the following form:

$$\frac{dN}{dt} = rN\ (K-N)/K$$

where N is the number of individuals, t, the time, r, intrinsic rate of population growth, K, carrying capacity and $\frac{dN}{dt}$ represents the rate of change in population size. Verhulst's contribution was widely recognised after Pearl and Reed published their paper in 1920.

Most of the studies on population in 19th and 20th centuries have been done using animal populations. A theoretical model for plant populations was proposed for the first time by Nägeli (1874). Turesson (1922, 1925) established another landmark in population research by recognising the existence of micro populations or ecological races within a species population growing in contrasting micro climates.

Elton (1933) proposed the term "population dynamics" which according to him referss to the field of study "concerned with rates of increase, fluctuations in numbers and relation of problems of numbers to the environmental factors which influence the population". In the year 1928, Chapman introduced the two new terms "the biotic potential" and the "environmental resistance" which are widely used in population ecology. In his classical paper Chapman stated "it seems evident that we have in nature a system in which the potential rate of reproduction is pitted against the resistance of the environment, and that the quantity of the organisms which may be found, is a result of the balance between the biotic potential and the environmental resistance." Based on experimental data he derived a formula establishing a relationship between the two:

$$C = B_p/R$$

where C is the number of existing organisms, B_p, the biotic potential and R, the environmental resistance. He concluded that whatsoever the potential rate of development of an organism may be, its environment offers sufficient resistance to multiplication to cause the number to remain constant.

The work of Sukatschev (1928), Tadaki and Shidei (1959), Harper and Gajic (1961), Harper and McNaughton (1962) and Raynal and Bazzaz (1975), opened new dimensions in population ecology with a conclusion that populations do have a self-regulatory mechanism. The rate of population growth is generally expressed as the increase in number of individuals per unit time and can be estimated if the data on birth, death, immigration and emigration rates are available. Thus, Lotka (1931) and Volterra (1931) calculated the intrinsic rate of change based on these parameters which was later confirmed by Gause, a Russian biologist, in the year 1934. Gause (1934) put forward the famous "Gause hypothesis" stating that "no two species can share exactly the same ecological niche for indefinite period of time; eventually one will replace the other". Further, he concluded that the displacement of one species by the other is inevitable if one of them has an advantage over the other. The displacement principle has been studied since then by many (Park, 1954; Frank, 1957; Harper, 1961; Tantawy and Soliman, 1967).

Part of the Darwinian tradition in the study of plant population dynamics is the observation of the behaviour of plants in permanent plots over a period of time. Charting the fate of individual plants (to grow, to flower, to remain vegetative, to die) has been undertaken by few people. Observations on the longevity of populations, rates of turnover in their vegetative and reproductive composition, etc. are extremely laborious. The work of Tamm (1956), Sagar (1959) and the Moscow School of Rabotnov and coworkers since the 1940's hint at regularities in natural population dynamics that are quite surprising. There is an impressive tradition of field observation in Russia (Rabotnov and others) which has received too little attention hitherto. The long term data of foresters also provide valuable sources of information for the development of plant population dynamics (White and Harper, 1970) but they deal mainly with planted, managed systems. Some workers have been interested in quantitatively recording the spread of certain adventive species (Kent, 1956; Harper, 1970). The population changes of certain perennial plant species growing in meadow and forest community recorded by Tamm (1948, 1956) is one of the important and most systematic contributions. Tamm identified the position of each individual from year to year on permanent plots during a 14-year period and observed a constancy in numbers and a high rate of turnover.

Canfield (1957) presented data on the survivorship of the primary and secondary range grasses of south-eastern Arizona in relation to grazing and concluded that the mortality of "genets" of primary grasses was remarkably higher in the grazed area where the secondary grasses showed an increased life span probably due to reduction in the degree of interference from the primary grasses as a result of grazing. A similar type of work has also been done by Williams (1970). While studying the population structure and longevity of <u>Festuca rubra</u>, Herberd (1961) found that a single genet may spread over a vast area by extending its ramets through vegetative growth. Antonovics (1972) studied systematically the fate of the individuals from seedling stage onwards for their population flux, longevity of individuals, survivorship, natality and mortality and came to the conclusion that the individuals recruited at different periods, have different decay rates. Further, he observed that the different populations, have different longevity depending upon their adaptation to a particular habitat and suggested that difference in longevity of individuals of different populations may be related to the environmental conditions.

The population studies of plants received the much needed impetus from the works of Harper and his coworkers during the last two decades. A number of plant biologists have also followed the trend and over the past 12 years a good amount of work on plant demography has been accumulated. A more detailed study of demographic nature has been recently made by Sarukhan and Harper (1973) with three species of Ranunculus, R. acris, R. bulbosus and R. repens in a grassland situation considering many important aspects of population ecology. Sarukhan and Gadgil (1974) analysed mathematically the data of this paper. Mack (1976) studied the survivorship of Cerastrium atrovirens and Hawthorn and Cavers (1976) studied the population dynamics of the perennial herbs, Plantago major and P. rugelii.

Callaghan (1976) suggested that the growth, reproduction and death of individuals in a plant population are affected by the environmental factors within the framework of their genetic programme. The environmental factors may be biotic such as grazing, predation and competition for the limited resources and abiotic such as cold, heavy precipitation, frost, storm etc. which destroy the populations catastrophically (Warren Wilson, 1967).

A great deal of work has been done on the mortality rates of the plant populations. Deevey (1947), on basis of the work with different populations, concluded that in general, the individuals follow three types of death and decay patterns; situations where there is high mortality in the juvenile phases (Hett, 1971; Sharitz and McCormick, 1973; Sarukhan and Harper 1973 ; Hett and Loucks, 1976) of the life when the plants pass through a transition stage between the dependence of seedlings on seed food reserve and their establishment when they become self-dependant. However, a change in climatic or edaphic factors may also play a major role (Tazaki, 1960; Peterson, 1966; Cavers and Harper, 1967; Friedman and Orshan, 1975; Marquis, 1976). In contrast to the seedlings, the adults show a constant risk of death throughout their life-span giving a negative exponential curve (Tamm, 1956; Rabotnov, 1958; Sagar, 1959; Foster, 1964; Antonovics, 1972). The individuals with long life span generally show a third category of survivorship with higher mortality in the last part of their life. The curves which represent these three different mortality patterns are the Deevey Type I, Type II and Type III curves of mortality.

The studies on the population dynamics of the perennial plants, are often not attempted as it is difficult to determine their exact age due to the lack of any reliable technique for estimation. Various methods used to determine the age are based on anatomical and morphological features such as growth rings in stem or rhizome and leaf scars on the rhizome. Pigott (1955) found that the age of Cirsium acaulon can be accurately estimated by counting the number of leaf scars on the rhizome. Kerster (1968) and Levin (1978) have considered the rings present in the corm of Liastris aspera for determination of its age. However, Werner (1978) did not agree with them and suggested that there is no relation between the age and number of rings in the corm of Liastris aspera. The most reliable method for estimating the age of perennial herbs, is to follow the fate of labelled seedlings or tillers of known age in permanent enclosures. This method has been successfully used by Tamm (1956, 1972a, 1972b).

An individual plant in the population, is comprised of various parts like stem, leaf, root, rhizome buds, tillers and flowers etc. Some of the latest trends in population ecology are to study the dynamics of these parts of sub-population level. Thus, Saeki (1960) in Phaseolus viridissimus and Nicotiana tabacum and Gill and Tomlinson (1970) in Rhizophora mangle studied the dynamics of leaf production. Halle and Oldeman (1970) worked on the dynamics of the branches, leaves and buds of a number of tropical trees. Gill (1971) observed the dynamics of buds in Fraxinus americana. Kays and Harper (1974) studied the change in population of Lolium perenne at the two levels of population organisation. Such a study was also undertaken by Ogden (1974) in Tussilago farfara. Bernard (1976) studied the life history and population dynamics of shoots of Carex rostrata and noted a constant rate of death with very high turnover rates. A comprehensive account of the latest investigations in the field of the dynamics at sub-population level has been reviewed by Harper (1978).

A population may be comprised of genets which include the seedlings and the adults besides ramets. According to Harper and White (1974), while studying the age-structure of the population of a perennial species, the seedling population may or may not be considered depending upon the observation period of the year as the number of seedlings in most of the species fluctuate in time and space with 100% mortality in perennial grasses (Putwain et al., 1968). Richards (1952), Emlen (1972) and Schaal (1978) suggested that the unstable age-structure of plant species may be observed due to large environmental fluctuations that may occur during critical periods in the plant's life. According to Rabotnov (1945, 1950a, 1950b, 1969), a coeno-population is characterised by various age groups of individuals based on the four main periods of life of the plants reproducing by seeds. These periods are (i) the period of primary dormancy, (ii), the virginal period, (iii) the generative period and (iv) the senile period. A detailed account of the longevity of the shoot modules has been presented by Noble et al. (1979) and Harper and Bell (1979).

The seeds constitute the dormant phase of the populations and a study pertaining to their dynamics in time and space, is of immense importance in understanding the population behaviour of a plant species. The role of the seeds in early phases of primary and secondary successional processes is of special significance as also emphasized by Oosting (1942), Keever (1950), Egler (1954), Bazzaz (1968, 1973), Holt (1972), Johnson (1975), and Archibold (1979).

The associated vegetation may also exercise considerable influence in regulating the population (Odum and Odum, 1959; Harper, 1964) as the natural habitats of the species are mostly shared by many thickly populated species affording resource competition through inter-specific interaction though intra-specific competition may also play a significant role (Ramakrishnan and Jeet, 1973; Ramakrishnan and Gupta, 1981). Poor seedling establishment has been reported in established communities by Tamm (1956) and Cavers and Harper (1967). Putwain and Harper (1970) and Dwivedi and Tripathi (1980) found that amongst the associated species, grasses exercise greater regulatory influence compared to dicots. Sagar (1970) noticed increased vegetative and reproductive growth of Plantago lanceolata when the associated vegetation was removed. Established plant populations of a species also affect the newly recruited seedlings of their own species (Friedman, 1971; Andel and Rozema, 1974; Gupta and Tripathi, 1979; Yadav and Tripathi, 1981).

Intra-and inter-specific population behaviour:

The behaviour of the individuals of one or the different species growing together and interfering with each other's mechanism of population growth is of great significance. The vegetation composition of an area can partly be considered the resultant of the competitive abilities of the individuals which in turn might be influenced by their environment.

The term "competition" refers to the greater growth in vigour of some individuals as compared to others when a certain requirement is in short supply for one or more individuals. Thus, competition results when the two organisms seek the same resource which in turn is below the combined demand of organisms (Donald, 1963). The competition is known to exist when growth of either one or both the individuals is reduced compared to their growth in isolation (Bleasdale, 1960). The degree of interference also depends upon the distance between the individuals. The extent to which the two individuals may compete also depends to a great extent upon their ecological amplitude and efficiency of their overall physiological makeup in a particular environment. Competition generally occurs in its severest form when physiology and the growth habits of individuals are similar and their niches overlap completely (Clement, 1929; Odum, 1969; Ramakrishnan, 1965a, 1970; Ramakrishnan and Gupta, 1972; Ramakrishnan and Jeet, 1972).

Thus inter-ecotypic competition between different ecotypes in marginal areas is a mechanism by which the populations in contrasting habitats are kept apart (Ramakrishnan, 1965a, 1965b, 1965c, 1966; Ramakrishnan and Nagpal, 1973; Ramakrishnan and Kumar, 1976).

Competition can be intra-specific i.e. between the individuals of the same species or inter-specific i.e. between two different species (Odum, 1969). Harper and Chancellor (1959) introduced the term "self-thinning" and "alien-thinning", the former describes the reduction of chance of a seed forming a mature plant due to increase in the density of the individuals of the same species while the latter describes the reduction in chance of a seed forming a mature plant due to increased density of associated species.

Competition involves both the root and the shoot system for water, nutrients and the light. Bergh van den (1968) introduced the term "space" as a combined expression of all the resources required by the plants.- Tekekawa (1968) found that the competition for nutrients was the main reason for the decline in the yield of rice when rice plants were grown together with Potamogeton distinctus. Ramakrishnan (1961) has demonstrated that root competition in the two ecotypes, the red and green form of Euphorbia thymifolia, competing with each other does not permit the obligate calcifuge (green form) to establish seedlings in the calcareous soils.

The competition involving shoot system is for light due to the overlapping growth of the plants; as a result one species succeeds. at the expense of the other (Harper, 1964). Black (1957, 1958, 1960) noted an increase in the competitive vigour of the plants grown from bigger seeds compared to those from smaller seeds of Trifolium spp. Ennik (1960), from his competition studies on pure and mixed stands of Lolium perenne and Trifolium repens under low and high light intensities found the replacement of grass by clover under high light intensities, but under low light intensities the two species tended to stablize; those with excess of clover tending to increase the grass content and vice versa. In the latter case it is belived that the stabilizing influence between the two species is due to differential requirements of the two for nitrogen.

As an agronomic problem intra-specific interference has ~~receive~~ received much momentum with respect to (i) reactions of plants to density which determines crop yield in pure stands and (ii) mutual interference between species under the the condition of mixed cropping. Yoda et al. (1963) concluded that:

(i) the chance of a seed producing a mature plant declined with increasing density,

(ii) irrespective of the density of the seeds sown, there is a maximum population size attained and densities beyond this level can not be realized no matter how many seeds are sown,

(iii) the densities in overcrowded populations converge with the passage of time irrespective of the differences in initial density. The converging densities are always lower on more fertile soils,

(iv) this convergence is related to plant size so that plants having a certain average size always maintained more or less similar levels of surviving density regardless of this difference in stand age, initial density and fertilizer level.

Harper (1961), Ramakrishnan and Kumar (1971), Ramakrishnan (1971) and Ramakrishnan and Jeet (1972), concluded that with increase in density the proportional allocation of assimilatory products to aboveground organs of plants may change resulting in less reproductive output.

A few mathematical derivations related to the density and the yield response of crops, have been formulated. Amongst the most successful of these have been various forms of reciprocal laws:

$$\frac{1}{w} = a + bx$$

where x is the density and w, the mean plant weight.

Yoda *et al.* (1963) for the first time mathematically expressed the process of self-thinning and found that numbers of surviving plants could be related to its mean weight as:

$$W = C_p^{-\frac{3}{2}}$$

Where p is the density of surviving plants and W is the corresponding mean weight, the value of C varies with species. This was later confirmed by White and Harper (1970).

Individuals may respond to density by either a reduction in their vegetative or reproductive growth or the reduction in the chance of the survival of the individuals (Harper and Gajic 1961; Ramakrishnan and Kumar, 1971a, b). Sukatschev's attempt (1928) was the first pertaining to the self regulatory mechanisms of plant populations. He concluded that under the conditions of both the increased density as well as ferilizer levels, the mortality of the individuals was enhanced.

Working with pure stands, Harper and McNaughton (1962) too reached similar conclusions. Koyama and Kira (1956) have shown that under conditions of density stress only, there is a forced showing of limited resources within a compensatory plastic reduction in plant growth. A greater mortality and/or plasticity in mixtures and monocultures respectively was noted by Ramakrishnan and Kumar (1971b) in wheat and *Cynodon dactylon*, Ramakrishnan and Kumar (1971) and Ramakrishnan and Gupta (1972b) on maize and *Cynodon dactylon* and in *Oryzopsis holiciformis* and *Avena sterilis* by Litav and Seligman (1969, 1970).

Many of the studies on population behaviour in mixtures are based on weed-crop interference. In general, weeds have greater potentialities to accumulate water, nutrients and light energy thereby decreasing the efficiency of crop production (Blackman and Templeman, 1938; Russell, 1961). In studies dealing with grass - legume associations different workers have shown the improved yield of the grass in the presence of legume (de Wit *et al.*, 1968; Bergh van den, 1968; Abu-Shakra *et al.*, 1969, and Reid, 1970). Such a response has also been shown in legume-crop interactions by Kapoor and Ramakrishnan (1975).

The famous experimental model of de Wit (1960) marked the beginning of a new era in the studies of behaviour of two species in mixtures. The model facilitates the study of the performance of two species in pure and mixed stands with varied proportions of the species, keeping the overall mixture density constant. The behaviour of a species is compared in pure stands with its performance in variously proportioned mixtures and mutual aggressiveness of the two species is measured. de Wit *et al.* (1960) discussed different situations and suggested the following models.

(i) Simplest form of competition occurs if two species compete for the same space.

(ii) This model occurs when two species affect each other only by crowding for the same space, finish their growth in the same length of time and have similar growth curves.

(iii) This more complex model occurs when two species having the same growing period crowd for the same space but have dissimilar growth curves.

(iv) A very complicated pattern of competition in this model, if two species do not crowd for exactly the same space. This may occur if some requisite obtained from the soil limits the growth, and one species can explore the soil to a greater depth than the other. The same applies if one species has a more prolonged growing period. Such a stable equilibrium may also be found if one of the two species crowding for space, is benefitted from the presence of the other. Competition between grass and clover is an example of this model.

(v) This model is applicable if one of the two species hampers the growth of the other, not only by crowding for same space, but also by some processes such as the production of toxic substances harmful to the other.

Reversal of habitat performance has also been shown by Harper and Chancellor (1959) who grew Rumex species on clayey soil with or without Lilium perenne and found that in the absence of the grass, the establishment of Rumex crispus and R. obtusifolius was more successful under maintained water table. In the presence of the grass, the most successful establishment of R. obtusifolius occurred under freely drained conditions. The reason for such a reversal of habitat preference as in the case of R. obtusifolius is yet not clear. However, in the case of Melilotus alba ecotypes the reversal of habitat preference is definitely related to their differential response to nutrients, particularly calcium (Ramakrishnan, 1968a, 1968b, 1970).

Present work:

Slash and burn agriculture (locally called "Jhum") is a predominant form of agriculture in north-eastern hill region of India. It involves the slash and burn technique of clearing the forest, cropping for a year or two and then abandoning the land for forest fallow development, for the restoration of soil fertility (Ramakrishnan et al., 1980).

In the past, the jhum cycle (the intervening fallow period before the same land is again cultivated) was of 20-30 years which was ideal not only for the restoration of soil fertility under a forested fallow but also for keeping the noxious weeds under control. However, in recent times there has been a considerable shortening of jhum cycle to about 4-5 years due to increased population pressure and changed land use practices. As a result not only the soil fertility recovery of the system is adversely affected but also large tracts of land have been taken over by ruderal weeds like Eupatorium odoratum L., Imperata cylindrica (L.) Beauv. var. major. Shortening of the jhum cycle has also led to almost pure stands of these weeds occupying vast tracts of land in an arrested stage of succession, being rendered useless for cultivation on this account.

The two weeds, namely E. odoratum and I. cylindrica are also the pioneers in croplands and in the fallows developing after slash and burn agriculture. Eupatorium odoratum, a native of Mexico, grows abundantly at lower elevations of Meghalaya (Kushwaha et al., 1981). It is a high-seeding species. Seeds are extremely light and are produced with pappus which help them in their dispersal to some degree. Seed germination in nature starts in May - June with the onset of monsoon. Large number of seedlings come up after few showers. The period between June and October represents the period of active growth, after which the plants start flowering. Maximum fruiting takes place in the month of January and seeds are mature by March.

The germination and growth behaviour of the populations of E. odoratum collected from seven localities from Old and New World Tropics, have been studied by Edwards (1974a, 1974b, 1975). He observed that these populations represent different ecotypes adapted to different climatic conditions. Further, he observed the ecotypic behaviour in the plants growing under different soil moisture conditions. The requirement of light for germination of E. odoratum has also been shown by Edwards (1974a) and Deb (1981). The development of embryo and female gametophyte has been described by Ghosh (1969). Khonglam and Singh (1980) reported that E. odoratum is a allohexaploid with chromosome number 60 and is apomictic. Yadav and Tripathi (1981) studied the dynamics and regulation of E. odoratum population and came to the conclusion that associated vegetation as well as the adults of the same species play a major role in the mechanism of population regulation. Kushwaha et al. (1981) studied the population dynamics of E. odoratum in early successional communities and concluded that:

(i) Survivorship of seedlings and adults decreases with the increase in the age of the community upto certain years.

(ii) the growth of the population is drastically reduced after about about 8 years of the growth of this species, when high canopy species shade it out in the process of secondary succession.

(iii) the fallows with maximum population density also suffered from maximum mortality probably due to intra-specific competition.

Imperata cylindrica has extensive underground rhizomes. The populations multiply through iterative production of tillers (leafy shoots). Besides, it also reproduces through seeds which are produced in large numbers and are widely wind dispersal.

There have been only few studies on the growth behaviour of this species. Richards (1952) and Nye and Greenland (1960) noted that under slash and burn agriculture in Africa, a short cycle is highly favourable for its vigorous growth compared to a long cycle when it gets eliminated from the system during the process of secondary succession (Beard, 1953). Schlippe (1956), while working on the ecology of "Zande system" of agriculture in Africa, observed that fire stimulates growth in this species. Further, he indicated that it may flower after dry season with little or no rain. In a recent study Eussen and Wirjahardja (1973) have even implicated allelopathy as an important factor for the success of this species.

However, these studies on the growth behaviour are relatively indadequate in the context of their widespread dispersal and success which pose serious agronomic problems. A study pertaining to the detailed analysis of their population growth providing information about that natality, mortality, survivorship and age-structure and the environmental factors which influence these population attributes may not only prove helpful in devising effective weed-control measures but also provide an insight into our understanding of their regulation in nature without environmental repurcussions.

For the present study, therefore, these two major early successional weeds with contrasting life cycle strategies were selected. A third, late successional species, Scleria tessellata Willd. was also selected to compare the population behaviour of these two early successional weeds with a late successional one occurring in contrasting environmental conditions. Apart from the population dynamics studies and a few other related to competition and response to different environmental conditions, a few selected agro-ecosystems have been considered from the point of view of their organization and yield patterns.